

A NEW COMMENSAL HYDROID OF THE MANTLE CAVITY OF AN OYSTER¹

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During the course of studies on the biology of the "mangrove oyster," *Crassostrea rhizophorae* (Guilding), in Puerto Rico, a number of oysters were found with the mantle cavity infested by an undescribed commensal hydroid (Mattox, 1949). The unusual habitat of this hydroid and its correlated adaptive features are not entirely unique, for two similar hydroids have been found in Italy, both also living in the mantle cavity of edible pelecypods. The hydroid here considered is recognized as belonging to the same genus as those found in Italy and is designated as *Eugymnanthea ostrearum*.

THE GENUS EUGYMNANTHEA

Palombi (1936) established the genus *Eugymnanthea* in naming a new species of hydroid found within the mantle cavity of the lamellibranch, *Tapes decussatus*, in Lago Fusaro, near Naples. This hydroid, *Eugymnanthea inquilina* Palombi is the generotype by monotypy. Cerruti (1941) described a similar hydroid from *Mytilus galloprovincialis* at Taranto. Unaware of Palombi's work he named this *Mytilhydra polimantii*, but upon learning of *E. inquilina* altered the name of his species to *Eugymnanthea polimantii*. Our species is similar to the other two and must be placed in the same genus.

The following are the features common to the three species of *Eugymnanthea* and constitute a definition of the genus. Athecate, solitary polyps, lacking hydro-rhizae and gonothecae, possessing a basal disc, a single whorl of tentacles, and producing from near the base, either sporosacs, or medusae of the leptomedusan family Eucopiidae. The three known species are commensal within the mantle cavity of pelecypods.

Eugymnanthea ostrearum nov. sp.

Description of the hydroid (Fig. 1 A). The polyps are simple, solitary, tapering toward the base, having a maximum length of 3.8 mm. (the average of 20 specimens, taken at random, was 1.54 mm.), having a maximum diameter of the column of 0.35 mm. There are as many as 35 filiform tentacles (average 30) in a single whorl. There is a slight intertentacular membrane which, on the largest polyp, was 0.18 mm. in width. The hypostome is a slightly elevated cone which does not extend beyond the limits of the intertentacular membrane. A striking feature is the basal or pedal disc, a flattened, slightly concave expansion of the base of the column.

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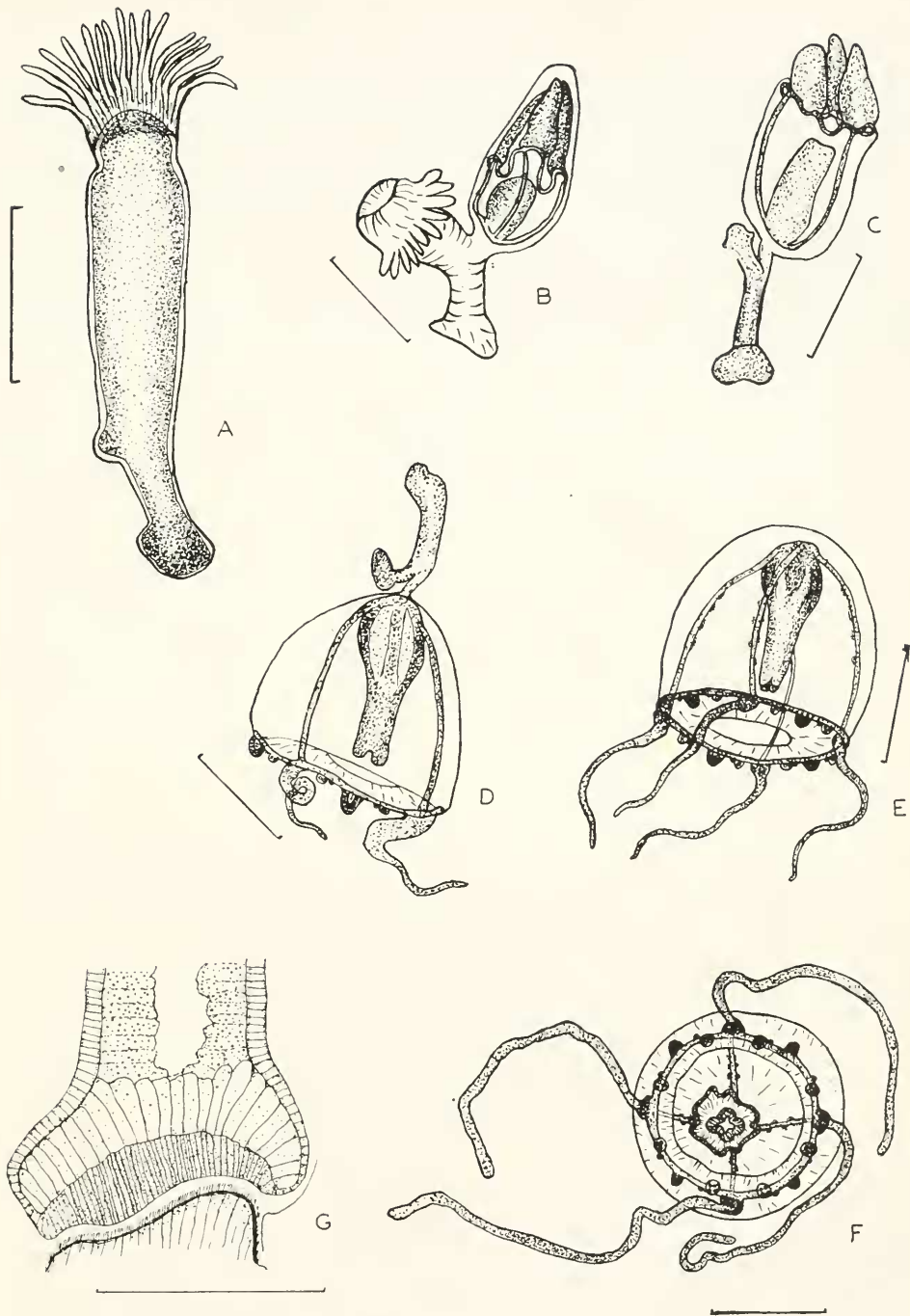


FIGURE 1. *Eugymanthea ostrearum* nov. sp. A: Polyp. B: Polyp and late medusa bud; the oral region of the polyp shows an unusual eversion. C: Medusa bud just before it began to swim and at a stage when the polyp had become reduced. D: Medusa two hours after it became free swimming, with the polyp still attached. E: Medusa one day after liberation. F: Medusa in oral view five days after liberation. G: The basal disc on the ciliated epithelium of the oyster; the scale line is 0.1 mm. for G. For A to F the scale lines are 0.5 mm.

There are no hydrorhizae, nor is there evidence of any periderm (perisarc). Nematocysts are present over the whole column and in batteries on the tentacles. They are small atrichous isorhizas, with capsules averaging 5 micra in length, and threads not much longer than the capsules. Buds near the base produce medusae.

Polyps are found adhering to mantle, foot, gills and labial palps of the "mangrove oyster," *Crassostrea rhizophorae* (Guilding), on the southern side of the Laguna Rincon at Boqueron, Puerto Rico.

Description of the young medusa (Figs. 1D, 1E, 1F). Medusae were kept in the laboratory for eight days. During this time no features appeared not observable soon after liberation. So far no medusae have been found in plankton samples from the Boqueron lagoon.

The young medusa is ovoid, slightly higher than wide, with a maximum height of 3.0 mm. There are four simple radial canals and a circular canal. Four simple perradial tentacles are borne on conspicuous hollow bases. At the time of liberation there are four interradial tentacle bulbs, and by the fifth day 8 very small adradial bulbs appear. Perhaps older specimens develop additional tentacles, but this has not been observed. There are 8 adradial statocysts, each with 2 to 6 statoliths. (These are perradial to the adradial bulbs when the latter appear.) There are no ocelli nor cirri. The manubrium is of moderate size extending about to the opening of the well developed velum. The mouth is surrounded by four simple lips. At the time of liberation there are no gonads; but specimens five days old show indications of gonad development on the oral surface of the radial canals. The nematocysts are similar to those of the hydroid. Specimens were obtained from the hydroid.

Cotypes are in U. S. National Museum: the medusae No. 49808, the polyps No. 49809.

In Table I we have compared the medusae of the three species of *Eugymanthea* as well as *Eucope parvigastra*, a medusa described by Mayer (1910) but one whose hydroid is unknown. Although such a comparison points up the obvious differences among these medusae, a consideration of these differences suggests that they are really quantitative and directly correlated with the time at which gonads develop. If gonads appear early the medusa remains small and tentacles and manubrium do not develop. On the contrary, if gonads develop late, the feeding parts of the medusa (tentacles and manubrium) are developed. Similar gonophore series are exemplified by other hydroids. The neatness with which *Eucope parvigastra* fits this series suggests that its unknown hydroid might be found in a bivalve of the Tortugas region. However, Dr. W. J. Rees (personal communication) has expressed doubt that there is any connection between *Eucope parvigastra* and *Eugymanthea*.

TAXONOMIC CONSIDERATIONS

Although *Eugymanthea* lacks periderm and most other features of typical Calyptoblastea, it produces a leptomedusa, and so must be regarded as a calyptoblastic hydroid. There are a few other hydroids which are athecate but produce leptomedusae. Some of these medusae belong to the subfamily Eutiminae, family Eucopiidae, and Stechow (1924) has proposed to place such hydroids in the subfamily Campanopsinae, of the family Heleciidae. This will not serve for *Eugymanthea ostrearum* since its medusa belongs in the subfamily Obelinae of Eucopiidae.

Possibly (as Palombi, 1936, suggests) *Eugymnanthea* should be placed in a new subfamily of Haleciidae, having affinities with Stechow's Campanopsinae. It is impossible to include the hydroid in any of the families of hydroids as defined by Fraser in "North American Hydroids" (1937, 1944). Since the absence of periderm is probably an adaptive character related to the commensal mode of living, little significance should be placed upon it in attempting to determine natural relationships.

Fortunately the medusa is readily classified. It fits the genus *Eucope* (Mayer, 1910) in all anatomical features. However, we regard it as generically different for the following reasons. Its polyp is so similar to that of *Eugymnanthea inquilina* and *E. polimantii* that it must be placed in the same genus. Their medusae do not fit the

TABLE I
Comparison of Medusae

<i>Eugymnanthea inquilina</i> Palombi	<i>Eugymnanthea polimantii</i> Cerruti	<i>Eucope parvigastra</i>	<i>Eugymnanthea ostrearum</i> nov. sp.
Naples, Italy	Taranto, Italy	Tortugas, Florida	Boqueron, Puerto Rico
Polyp in mantle cavity of <i>Tapes</i>	In mantle cavity of <i>Mytilus</i>	Polyp unknown	In mantle cavity of <i>Crasostrea</i>
Medusa 0.55 mm.	1.2 mm.	1.0 mm.	3.0 mm.
Spheroidal	Same	"Half-egg-shaped"	Same
8 adradial otocysts	Same	Same	Same
Not reported	3 otoliths, sometimes 1 or 2, rarely 4	Single spherical	2 to 6 otoliths
4 simple radial canals	Same	Same	Same
4 perradial tentacle bulbs	4 perradial bulbs 4 small interradial bulbs	4 perradial bulbs	4 well developed per- radial tentacles on large bases, 4 inter- radial bulbs, 8 small adradial bulbs
Gonads on radial canals. Large oval, shedding gametes before or soon after liberation	Same position. Same size as <i>E. inquilina</i> , hence relatively smaller, shedding gametes after lib- eration	Same position. Small	Same position. Not developed at time of liberation
Manubrium lacking	Manubrium lacking	"Very small, a mere tube cruciform in cross section"	Manubrium simple, extending to velar opening
Mouth lacking	Mouth lacking	Mouth present	Mouth present
Lips lacking	Lips lacking	4 simple lips	4 simple lips

definition of *Eucope* but are similar to *Agastra*. Furthermore none of the known hydroid stages of either *Agastra* or *Eucope* resemble the hydroid *Eugymnanthea*. Therefore we believe that the name *Eugymnanthea* should be applied to those medusae of the family Eucopiidae, subfamily Obelinae, which show resemblances to *Eucope* or *Agastra* and which are derived from polyps of the genus *Eugymnanthea* as previously defined.

REPRODUCTION OF THE HYDROID GENERATION

The method by which polyps produce other polyps has not been studied carefully in any of the species of *Eugymnanthea*. During the spring and early summer

Cerruti (1941) found groups of polyps, usually two or three, once as many as 7, attached to one another and arising from one basal disc. He says that these arise by budding and that later the polyps separate from one another. Palombi (1936) does not mention this type of reproduction but does show figures of two and of three polyps arising from a common basal disc. In some of our specimens a small polyp is joined to a larger one near the base of the latter. In others two polyps of nearly equal size share a common basal disc. Lacking direct continuous observations we cannot be positive, but all indications suggest the following method of reproduction. The second polyp arises as a bud near the base of the first, just as in related campanularians. The bud becomes a polyp which grows. Finally the two polyps split the basal portion of the column and the basal disc so that when separation occurs each obtains part of the basal disc. Such a combination of budding followed by fission does not occur in any other hydroid, as far as we know, but it is appropriate for a species in which the basal disc is so important.

Development of eggs has not been observed for any species of *Eugymnanthea*. However, Cerruti (1941) observed, in October, on the mantles of some of the mussels some little, somewhat spherical bodies and some very small polyps. He interprets the small bodies as due to the attachment of larvae which would soon transform into polyps.

DEVELOPMENT OF THE MEDUSA

Medusa buds arise singly near the basal end of the column, a polyp bearing only one medusa at a time. The changes of form and structure during development are similar to those described for other medusae having a comparable structure at the time of liberation. Since the other species of *Eugymnanthea*, unlike *E. ostracorum*, have gonads but no manubrium nor tentacles when liberated, it follows that our species is more like *Clytia*, for example, than it is like the other two species of *Eugymnanthea*, in respect to its developmental stages. (For *Clytia* see Goette, 1907.)

In the earliest stages of bud formation both epidermis and gastrodermis become modified. The epidermis becomes thickened as a placode (Fig. 2A). Its cells become less vacuolated and several layers deep. The gastrodermal cells beneath this placode have about the same height as those which lie between it and the basal disc, but are narrower. They have lost the vacuoles of typical gastrodermal cells but retain the conspicuous granules. By the time the placode has thickened so that it is about five cells thick, its cells have lost the vacuoles, and the underlying gastrodermal cells no longer show the large granules (Fig. 2B). The small size of the cells, their loss of vacuoles and granules, the increase in size of the placode and its evagination as a young bud all reflect high mitotic activity. This has been clearly shown for other developing medusa buds by Berrill (1949a, 1949b).

The mantle and mantle cavity are established very early through the rearrangement of epidermal cells of the placode. The mantle (sheath, ectotheca) is an epidermal covering of the developing medusa characteristic of most calyptoblasts. It is described as arising by delamination of irregular thickenings of the epidermis (Goette, 1907). In *Eugymnanthea* this delamination has more orderliness and precision than has been reported in other cases. Figure 2B shows an early mantle cavity. The cells which line the cavity appear to be oriented with reference to it,

and its extension the result of their rapid multiplication. The mantle itself is two cell layers thick. The outer cells soon become vacuolated and continuous with the epidermal cells beyond the placode; while the inner cells resemble those of the rest of the placode with which they are continuous around the circumference of the mantle cavity (Fig. 2C). The mantle becomes thinner as the medusa develops and is ruptured at the time of liberation.

The epidermal cells of the placode soon alter their arrangement to produce the entocodon within which the prospective sub-umbrella cavity is formed. Figures 2D and 2E illustrate this stage. The entocodon is quadrilateral in cross section. It is flanked on its slightly concave sides by the endodermal sacs destined to form the radial canals, and is bordered at its corners by a single layer of endodermal cells which are continuous with the endodermal sacs. Subsequently the sub-umbrella space expands; the manubrium arises and extends into it. By these processes and the establishment of tentacle bases, velum and otocysts, the stage is reached, just prior to liberation of the medusa, illustrated by Figure 2F. The four tentacle bases are much larger than in the other species of *Eugymnanthea* and most other calyptoblasts. They have about the same proportions as those of *Clytia* (Goette, 1907).

During the late stages of the development of the medusa there is a striking reduction in the size of the polyp. It loses its tentacles by reduction and resorption, and diminishes in size to less than one fourth of the original size. When the medusa ruptures its mantle, begins to pulsate, and becomes free swimming it carries the small remnant of the polyp with it. This remnant drops from the medusa soon after the medusa begins its free life. The reduction of the polyp is illustrated in Figures 1C, 1D, and 1E. Palombi (1936) found a similar reduction of the polyp during the formation of the medusoids of *E. inquilina*, but Cerruti (1941) found no such reduction in *E. polimantii*. An analogous reduction occurs in *Obelia* and in *Campanularia* (Berrill, 1949b; Crowell and Rusk, 1950), where blastostyle production often causes regression of the nearby hydranths. A similar regression of the polyp of *Craspedacusta* accompanies the production of a medusa (Payne, 1924).

In most colonial calyptoblastic hydroids the production of a gonangium requires the cooperative support of many feeding hydranths. A single small polyp, like that of *Eugymnanthea*, is probably unable to furnish sufficient substance for the construction of a gonangium. As an alternative it produces a single medusa with a morphogenesis like that of one of the medusae arising on a blastostyle.

THE COMMENSAL RELATIONSHIP

Oysters containing *Eugymnanthea* have been found at all seasons in the Boqueron lagoon. In 11 random samples, totalling 138 oysters, and extending from January to December of 1950, 12 per cent contained polyps. In heavily infested oysters the polyps are attached chiefly to the inner surface of the dorsal region of the mantle, but are also found on the foot, gills and labial palps. Some are scattered and isolated, others are found in large groups. Some oysters contain only a few polyps, others many. In one oyster 4.5 cm. long, 210 polyps were counted.

The most striking feature of *Eugymnanthea* is the conspicuous basal disc by which the polyps are enabled to remain attached to the host tissue. In detached specimens the disk appears circular and concave. In prepared sections, where it is attached,

it shows both a tendency to be concave and at the same time to modify its shape to conform with folds of the host epithelium. The epidermal cells of the disc are high, narrow, heavily stained (hematoxylin), and non-vacuolated (Fig. 1G). The gastrodermal cells of the disc are large and lack the conspicuous granules of unmodified gastrodermis. Although the disc resembles the pedal disc of hydra superficially, it seems clear that the ability to adhere is not due to secretion of a mucous material which could hardly be effective on the slimy epithelium, but rather to suction achieved through the muscular activity of one or both cell layers. In living oysters the polyps sometimes become detached, then re-attach at other sites.

Specimens are attached both on naked and on ciliated epidermis of the host. The cilia do not appear to be damaged. There is no evidence of penetration into host tissue nor alteration of it. Cerruti (1941), in *E. polimantii*, reports loss of cilia of the mantle where the discs attach, and the presence of granules in the cytoplasm of the epithelial cells of the host mussel. The disparity between our observations and his may be due to a real difference between the hydroid-host relationship in the two pairs of species, or it may be that such damage may sometimes occur, sometimes not, in both species.

The mantle cavity of a pelecypod is obviously an excellent dwelling place for a small hydroid. It provides protection and an abundant current of water. The only disadvantage would seem to be the difficulty in remaining there. Most hydroids could not do so; *Eugymnanthea* has the necessary adaptation, the basal disc. Periderm (perisarc) is unnecessary in such a small and well protected polyp. Stolons (hydrorhizae) would be useless. The modifications in the methods of producing additional polyps and in producing medusae, discussed earlier, are also appropriate to the peculiar habitat of this hydroid.

We wish to thank Dr. W. J. Rees of the British Museum for helpful suggestions, particularly in reference to the taxonomy.

SUMMARY

1. *Eugymnanthea ostrrearum* nov. sp. is a small, solitary hydroid living, attached by a basal disc, within the mantle cavity of the oyster *Crassostrea rhizophorae* (Guilding), in Puerto Rico. Two similar species have been described from Italy.

2. Its taxonomic position as a hydroid is somewhat uncertain since it lacks nearly all of the characters used in hydroid classification. It produces a leptomedusa similar to *Eucope*, and as a medusa belongs to the family Eucopiidae, subfamily Obelinae.

3. It shows the following features which may be regarded as adaptations appropriate to its commensal existence within the mantle cavity of the oyster: basal disc, absence of perisarc and stolons. Since the polyps are solitary there can be no gonangia.

4. Polyps are produced by budding followed by a fission of the basal disc. The development of the eggs has not been studied.

5. The development of the medusa is not unusual except in the way in which the mantle is established. It arises in a more sharply defined manner than that described in other forms by previous observers.

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